Welcome Swallows (*Hirundo neoxena* Gould) in New Caledonia

by

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The only Swallow known from the French Territory of New Caledonia and its Dependencies was the dark-bellied *Hirundo tahitica subfusca* Gould, whose range extends from Moala and the Fidji Islands (*H. t. tahitica* being the form that occupies the Society Archipelago) westwards to the New Hebrides and the Solomons.

This bird had been seen in the three Loyalty Islands, and had been found breeding on the island Ouvéa (Macmillan, unpublished Notes, in the A. M. N. H. New York; and Warner 1947). It had been noted, only once to my knowledge, in New Caledonia itself by E. L. L. Layard (1882, P. 503), who wrote (under the head-line *Hirundo tahitica*): "On the 26th November 1879 we saw a young bird flying round the office of the mailsteamer in ... Nouméa ... After assuring ourselves the identity ... (we) returned next day with our collecting gun ... in vain ..." (1882 p. 503).

I saw *H. tahitica subfusca* at St. Joseph, Ouvéa, circling around the village and above the lagoons, everytime I stayed there from 1975 to 1978; and I examined a few nests under eaves in buildings, not occupied at the times of my visits which took place from August to November.

Later I was intrigued, when doing field work in the Northern part of New Caledonia proper (Grande Terre) by some ten white-bellied, long-tailed Swallows flying for an hour or two, 1 to 3 meters high above the surface of a large lagoon, in the extensive Diahot Basin. The water at this place is rather muddy and just a little brackish. The Swallows would go down and touch the water level for a leap. They also used to perch for one minute, each every 10 or 15 minutes, on wooden poles less than 1 meter high above the water that had been planted there by fishermen. There were no Swifts above the lake on that day. One specimen was obtained and proved to be *Hirundo neoxena*. This was on July 17, 1976.

The same species was identified again on the west coast of N.C., south of La Foa in the early morning of January 28 1978: a pair circling in double loops 1 or 2 meters high above shallow waters between mangrove and sandy beaches. An other observation was made in February the same year, at Koné, West coast: 4 or 5 birds flying 10 meters high above the houses before sunset.

It will be of interest to see whether this species is only a casual visitor coming from the West or South West (Australia ...) or whether it is, or will soon be, breeding in New Caledonia. There are a handful of New Caledonian birds whose origin is evidently Australian, like *Myzomela sanguinolenta caledonica* and *Accipiter fasciatus vigilax,* this last one reaching the Loyalty Islands and even the Southern New-Hebrides. Quite recently (1978) *Gallinula tenebrosa* has been discovered in New Caledonia by Mr. Hannecart. If *Hirundo neoxena* becomes established in the country it will fill there the same ecological niche that is occupied by *Hirundo tahitica* a hundred kilometers to the East on Ouvea Island.

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A review of *Brookesia* systematics with special reference to lung-morphology (Reptilia: Sauria: Chamaeleonidae).

by

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Introduction

In the preface to his compilation of chameleon species Mertens (1966) briefly refered to the uncertainties concerning the validity of the various (sub)genera within the family Chamaeleonidae distinguished by previous authors. The uncertainties result from the lack of knowledge as to the variation of the various taxonomic characters in the majority of species. In spite of the lacunae previous systematists carried through systematic alterations such as assignment of the same species to different genera, erection of new genera etc. Mertens (op. cit.) is more reserved and in his list he only recognized two genera, viz. *Brookesia* Gray, 1864 comprising the pygmy chameleons and *Chamaeleo* Laurenti, 1768 comprising the ''ordinary'' chameleons. The other names are regarded as synonyms. Mertens stressed, however, that detailed studies of all known species might very well lead to the restoration of the various (sub) genera.

Although numerous articles on *Brookesia* have been published before and since 1966, a critical review of *Brookesia* systematics is still not available. Moreover, in spite of Mertens' suggestions, a comprehensive morphological study has not been carried through either. Therefore, in this introduction the confusing nomenclatoral history of the genus *Brookesia* is reviewed and the reliability of the taxonomic characters discussed. Moreover, some personal observations on these characters are included in the discussion. Subsequently the results of a detailed anatomical study are presented and discussed in relation to the systematics.

The status of the genus *Brookesia*

The members of the genus *Brookesia* show a remarkable variation in external characters: notably simple or bicuspid claws, smooth or spinose scales on the soles of the feet and the presence or absence of transversal paravertebral spines. On account of this variation, this group of pygmy chameleons has previously been split into various genera, viz. *Brookesia* Gray, 1864 comprising all Malagasy pygmy chameleons; *Rhampholeon* Günther, 1874 comprising all forms of continental Africa; *Leandria* Angel, 1933 a monotypic genus for the species *perarmata* and *Evoluticauda* Angel, 1942 including next to the former *Brookesia minima* Boettger, 1893; *B. nasus* Boulenger, 1887 and *B. tuberculata* Mocquard, 1894 from Madagascar, all African forms that previously constituted *Rhampholeon*.

According to Boulenger (1887) and Werner (1911 b), *Brookesia* as well as *Rhampholeon* are characterized, in contrast to *Chamaeleo,* by the possession of a short tail and spinose soles. They can be distinguished from one another by the bicuspid claws found in *Rhampholeon.* Angel (1929) demonstrated, however, that next to spinose soles smooth soles occur in *Brookesia* as well. Loveridge (1933) endorsed this view and found that the same applies to *Rhampholeon.* Moreover, he established several species of *Rhampholeon* to have simple claws. It follows, that simple or bicuspid claws cannot be used to distinguish the two genera, as it would place closely related East African species into different genera. Therefore he only recongnized *Brookesia* as a valid genus, including the other name as a synonym. Loveridge (1953 & 1957) subsequently regarded *Rhampholeon* at the most as a subgenus of *Brookesia* on account of anatomical differences described or rather supposed to be described by Parker (1942). Loveridge (1951) held a different opinion with regard to the scope and consequenses of Parkers studies and why he changed his mind is unclear to me. Parker is quite unambiguous ("Sufficient osteological material is not available...") and as I read it, he only studied the anatomy of *Rhampholeon* (sic) *spectrum* Buchholz, 1874 and *Brookesia superciliaris* (Kuhl, 1820). He *assumed* the anatomy of the other species mentioned to be conform to the anatomy of either these two species. So in my opinion Loveridge (1951) was quite right in his first evaluation of Parkers work when he stated: "Until, however, it has been demonstrated that the skeletal differences he described are generally characteristic of their respective groups, instead of an individual species selected from each, I continue to refer all pygmy chameleons to the older name *Brookesia.*" Nevertheless, some authors, viz. de Witte (1965), Broadley (1971) and Wright & Broadley (1973) thought the observations of Parker (1942) sufficient to retain *Rhampholeon* as a valid genus. Occasional personal examinations of everted hemipenes (furnishing very helpfull taxonomic characters) of various continental *Brookesia* seem to support this view. These organs differ markedly from those of *Brookesia* from Madagascar and look more *Chamaeleo*-like, i.e. being strongly ornamented with long apical (calcarous?) spines.

Angel (1933) established the genus *Leandria* for a highly ornamented pygmy chameleon from Madagascar, viz. *perarmata.* He stressed its close resemblance to *Brookesia,* notably *B. ebenaui* (Boettger, 1880), although various characters in common are much more developed and modified. Subsequent authors included this species in *Brookesia,* probably and in my opinion rightly so, because they regard it to represent the culmination of the bizarre ornamentation of *Brookesia* and the differences not sufficient to justify the erection of a new genus (cf. Mertens, 1966 and Brygoo, 1971).

In 1942 Angel endorsed Loveridge's view concerning the synonomy of *Rhampholeon* with *Brookesia.* Simultaneously he created the genus *Evoluticauda* comprising both Malagasy and African species (of the *minima*-group and the old genus *Rhampholeon* respectively), that can be distinguished from *Brookesia* sensu stricto by the absence of transversal paravertebral spines. However, in my opinion an analogous reasoning as was given by Loveridge in 1933 applies here: if we define genera on the basis of absence or presence of transversal paravertebral spines, more or less related Malagasy species are then divided and, moreover, the species of the *minima*-group are grouped with species that are obviously not so closely related, viz. the African species. Loveridge (1957) and Mertens (1966) indeed consider *Evoluticauda* but another synonym of *Brookesia*, although without argumentation. This view is confirmed by the studies of Brygoo (1971) and Brygoo and Domergue (1969, 1974), from which it appeared that in various species of the *minima*-group the transversal paravertebral spines may be indicated, as for example in *B. ramanantsoai* Brygoo & Domergue, 1974, or even well developed be it few in number as in *B. dentata* Mocquard, 1900[1]). Hemipenial characteristics also emphasize the affinity with the other *Brookesia* of Madagascar (Brygoo et al., 1969 and Ramanantsoa, pers. comm.). However, major taxonomic alterations concerning the *minima*-group (revision of the known species, description of various new species and perhaps even a genus-status for this group can be expected in the near future (Ramanantsoa, in press). In the present paper, however, the nomenclature as proposed by Mertens (1966), Brygoo (1971) and Brygoo, Blanc and Domergue (1972) is endorsed and taxonomic alterations postponed until more is known about the variation of anatomical characters within the whole group.

The relation of *Brookesia* to *Chamaeleo*

The pygmy chameleons (*Brookesia*) resemble the ordinary chameleons (*Chamaeleo*) in many respects, but mostly they can easily be distinguished at first sight. Nevertheless the differences described in literature are not very convincing to say the least. According to Loveridge (1933) and Brygoo (1971) the two genera are characterized as follows:
Tail non-prehensile, always shorter than the body (head included); smooth or spinose soles and simple or bicuspid claws ... *Brookesia*.
Tail prehensile, usually as long as, or longer than the body (head included); smooth soles and simple claws ... *Chamaeleo*.

The last two characters mentioned cannot be conclusive as in several *Brookesia* species both simple claws and smooth soles are found, e.g. *B. temporalis* (Matschie, 1892)[2]); *B. nasus* and the species of the *minima*-group. Of course these species have the additional "tail shorter than the body", but so do quite a number of ordinary chameleons as the "usually" already might have suggested. In various species this trait may occur occasionally, but it seems to be the rule in *C. anchie-*

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[1]) Brygoo & Domergue (1969) emphasize the unique position of the *minima*-group within the genus *Brookesia*, but change its composition according to morphological considerations, i.e. exclude *B. nasus* and include *B. dentata*. This does not, however, depreciate essentially the above argument.

[2]) These brackets indeed reflect that this species was once classed in *Chamaeleo*.

tae Bocage, 1872, *C. chapini* de Witte, 1964, *C. cristatus* Stutchbury, 1837, *C. gracilis etiennei* Schmidt, 1919, *C. namaquensis* A. Smith, 1831, *C. spinosus* Matschie, 1892, and various subspecies of *C. pumilus* (Gmelin, 1831) (vide Werner, 1902 a & b; Loveridge, 1933; Angel, 1942; Fitzsimons, 1943; de Witte, 1964 & 1965; Knoepffler, 1967 and Burrage, 1973). The present author also observed a tail shorter than the body in various specimens of *C. deremensis* Matschie, 1892 and *C. montium* Buchholz, 1874.

"Prehensile versus non-prehensile tail" is also questionable, as in *Brookesia* the tail can be considered to be prehensile as well, be it to a slight degree and in the tip only (cf. Mertens, 1951 and Brygoo, 1971). Angel (1942) stated: "... le caractère tiré de la queue *enroulable,* fortement préhensile, semble présenter une plus grande valeur systématique qui celui de la longeur de la queue elle-même...". However, Loveridge (1956) established the subgenus *Bicuspis* for a species (*marshalli*) that previously had been classed in *Rhampholeon* as well as *Chamaeleo* (see Boulenger, 1906 and Loveridge, 1951 respectively). He considered this species to occupy an intermediate position between the subgenus *Rhampholeon* and the genus *Chamaeleo* because of its bicuspid claws and prehensile tail (i.e. relatively long tail that can be coiled as well - Ch. K.). Thoughtfully Loveridge (1957) places *Bicuspis* in the synonomy of *Chamaeleo* and is followed by Mertens (1966). Broadley (1971) recommended, however, that *marshalli* be transferred from *Chamaeleo* to the genus *Rhampholeon.* The reason for this are the similarities in hemipenial and external morphological characters between *marshalli* and *R. platyceps* Günther, 1893. Moreover, the karyotype of *marshalli* and *R. spectrum* (Buchholz, 1874) are identical (Wright et al., 1873). Assuming for the time being only two genera within the family Chamaeleonidae these similarities justify that *marshalli* is included in *Brookesia.*

All in all we may well conclude that it is hard to differentiate between *Brookesia* and *Chamaeleo.* However, anatomical data may be conclusive in this matter. According to Brygoo (1971) the pigmentation of the testes seems to be a fairly constant character, i.e. in *Brookesia* the testes are invariably unpigmented whereas they are black in *Chamaeleo.* Presumably Brygoo only studied Malagasy *Brookesia,* but his view is confirmed by the absence of pigmentation in the species studied in the present paper, including two African forms, viz. *B. spectrum* and *B. brevicaudata* (Matschie, 1892). In contrast some quick checks at Museum A. Koenig in Bonn revealed, however, the testes to be black pigmented in the African *B. brachyura* (Günther, 1893), *B. marshalli, B. nchisiensis* Loveridge, 1953 and *B. platyceps!*

Data concerning skull- and vertebrae-morphology seem to be very promising, but as is the case in differentiating between *Rhampholeon* and *Brookesia,* the evidence is circumstantial, being the result of studies of too limited a number of species (vide Parker, 1881; Siebenrock, 1893; Werner, 1902 b; Methuen & Hewitt, 1914; Brock, 1941; Engelbrecht, 1951; Frank, 1951 and Broadley, 1971). Elucidating for that matter is the frequent classification of *Chamaeleo pumilus* and allies in a separate genus, mostly advocated by South African authors. The main reasons for this are differences in skull- and lung-morphology as compared with species of the *C. chamaeleon* group. In my previous lung-studies (Klaver, 1973 & 1977) I established, however, an extensive variation in lung-morphology within *Chamaleo*. Moreover, the lungs of *C. pumilus* and allies are by no means unique, the same type of lung is also found in other species. I then concluded that lung-characteristics cannot be used to validate the erection of a separate genus. The proposed splitting may nevertheless be correct in view of the skull-morphology, but the argumentation for that end would greatly improve by studying the variation of skull-morphology within *Chamaeleo* instead of emphasizing again and again well-established but fragmentary facts. So the general conclusion of this and the preceding paragraph is that if we want to establish separate genera within the Chamaeleonidae on account of anatomical considerations, comprehensive anatomical studies are a "conditio sine qua non". Ample material for skeletal investigations is hard to obtain from musea, as the material is lost for future morphological studies. Fortunately from the lungstudies on *Chamaeleo*, already mentioned above, it appeared that lung-characters are very helpful to systematics, whereas the necessary dissections are much less damaging. Therefore a comprehensive lung-study was expected to be likewise rewarding with regard to *Brookesia* systematics. The lungs of 22 of the approximately 31 species of *Brookesia* are described.

Material and Methods

The material studied belongs to the following institutions (indicated by the abbreviations in parenthesis): Etablissement d'Enseignement Supérieur des Sciences Agronomiques (EESSA), Antananarivo, Madagascar; Muséum Nationale d'Histoire Naturelle (MNHN), Paris, France; Musée Royal de l'Afrique Centrale (MRAC), Tervuren, Belgium; and Umtali Museum (UM), Umtali, Rhodesia.

The species examined are (grouped for the sake of brevity and clarity according to the two major areas of distribution):

African continent:

B. brachyura (Günther, 1893) UM 24852 ♀, Zomba, Malawi; *B. brevicaudata* (Matschie, 1892) MNHN 23-114 and 23-115 ♂♂, Teanga, Tanzania; *B. kerstenii* (Peters, 1868) MNHN 04-271 and 04-272 ♀♀, between Taita and the Kilimanjaro, Kenya-Tanzania; *B. marshalli* (Boulenger, 1906) UM 23279 ♀, Gleneagles, Inanga, Rhodesia; *B. nchisiensis* Loveridge, 1953 UM 24443 ♀, Misuku Hills, Malawi; *B. platyceps* (Günther, 1893) UM 25232 ♀, Madzeka Basin, Mlanje, Malawi; *B. spectrum spectrum* (Buchholz, 1874) MNHN 1968-84 ♂, Makokou, Gabon and MNHN 1973-1572 ♀, Bekinga, Gabon; *B. spectrum boulengeri* (Steindachner, 1911) MNHN 34-10 ♀, West Kitembo (1000 m alt.), Zaire and MRAC 26653 and 26654 ♀♀, Lutunguru (1500 - 1650 m alt.), Lubero terr., Zaire.

Madagascar:

B. antoetra Brygoo & Domergue, 1970 MNHN 1969-112 and 1969-113 (holotype and paratype respectively) ♀♀, Ambahona, Antoetra; *B. betschi* Brygoo, Blanc & Domergue, 1974

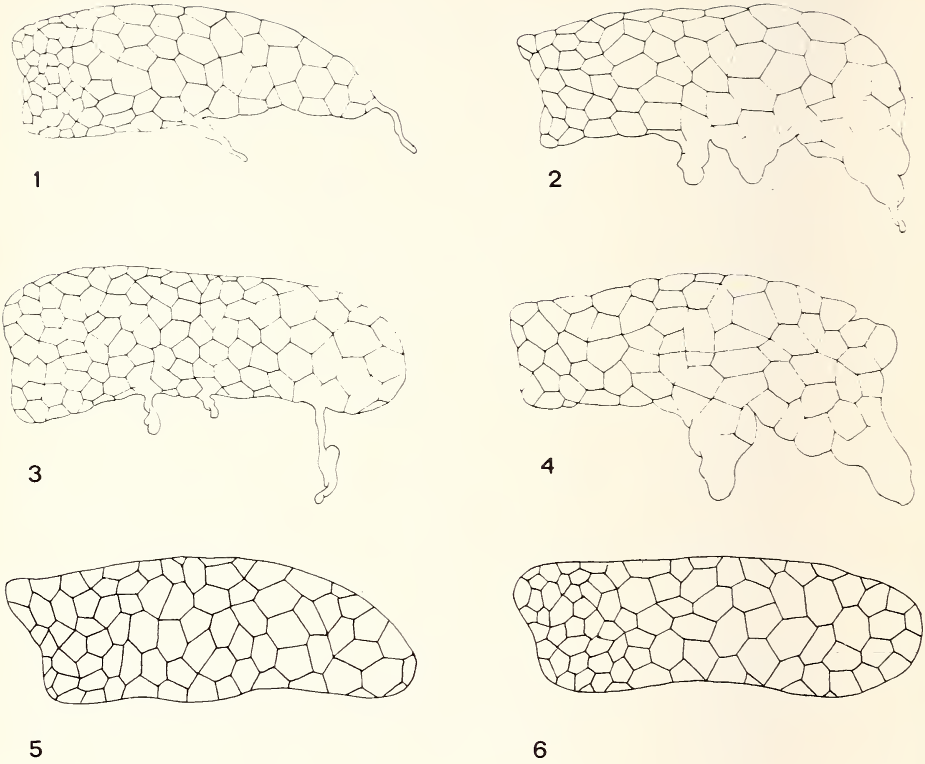
MNHN 1973-1180 ♂ and 1973-1182 ♀ (paratypes), Marojezy massif (1300 m and 1450 m alt.); *B. decaryi* Angel, 1938 MNHN 1974-227 ♂, Ankarafantsika massif; *B. ebenaui* (Boettger, 1880) MNHN 1974-222 ♂, 150 km south of Mitsingy, Kasijy forest, MNHN 1974-224 ♀, near Tuléar and EESSA 730 ♀, Antsalova and 732 ♀, Soalala; *B. griveaudi* Brygoo, Blanc & Domergue, 1974 MNHN 1973-1208 and 1973-1212 ♀♀, Marojezy massif (300 m and 600 m alt. respectively); *B. lambertoni* Brygoo & Domergue, 1970 MNHN 21-255 and 21-256 (paratype and holotype respectively) ♀♀, Fito region, West of Sihanaka; *B. minima* Boettger, 1893 EESSA 733 ♀, Soalala; *B. nasus* Boulenger, 1887 MNHN 1971-274 ♀ and 1971-275 ♂,Andringitra massif; *B. perarmata* (Angel, 1933) MNHN 83-32 ♀, Tsjandro, Antsalova; *B. spec* Ramanantsoa (in press) EESSA 731 ♂, Antsalova; *B. stumpffi* Boettger, 1894 MNHN 1973-1191 ♀ and 1973-1192 ♂, Nosy Lokoube; *B. superciliaris* (Kuhl, 1820) MNHN 1968-192 ♂, Maroantsetra and MNHN 94-249 ♀, locality unknown; *B. therezieni* Brygoo & Domergue, 1970 MNHN 1968-199 and 1968-200 (paratyes) ♂♂, locality unknown; *B. thieli* Brygoo & Domergue, 1969 MNHN 1968-194 and 1968-195 ♀♀, Périnet; and *B. vadoni* Brygoo & Domergue, 1968 MNHN 1968-5 (paratype) ♀, valley of the river Iaraka, Masvala peninsula.

For a detailed account of the dissections and the explanations of the terminology used, see my previous papers (Klaver, 1973 and 1977).

Lung-morphology in *Brookesia*

Only a few references to the lung-morphology in *Brookesia* are known from literature. In his paper on chameleon lungs, unfortunately overlooked in my previous studies, Werner (1911 a) described the lungs of *B. spectrum* and *B. stumpffi.* The lungs of these species look very much alike and consist of simple sacs that neither bear diverticula nor have septa to divide the lung-cavity. Alveoles cover the entire lung, but are weakly developed. Both species lack a gular pouch. Methuen et al. (1914) too found the lungs of *B. spectrum* to be simple without a trace of diverticula. They mentioned "*Brookesia* of Madagascar" to have similar lungs, but did not indicate the source of this information nor the species that were concerned.

The lungs of four species described in this paper were found to have diverticula. These species are: *B. brachyura, B. brevicaudata, B. kerstenii* and *B. nchisiensis* (cf. figs. 1, 2, 3 and 4 respectively). The shape of the lungs in the remaining species varies little. In some the distal part of the lungs is more tapered than in others, but probably this is due to differences in inflation at the time of preservation (cf. figs. 5 and 6). Weakly developed alveoles cover the entire inner surface of the lungs in most species. The only exception is *B. perarmata,* whose lungs have rather deep alveoles and are more spongy. Septa, i.e. relative large structures covered with alveoles and partitioning the lung-cavity, are absent. However, in some species the anterior part of the lungs possess both dorsally and ventrally various enlarged alveolar walls. *B. kerstenii* has four dorsal and two ventral enlarged alveolar walls, *B. marshalli* and *B. platyceps* have three dorsal and two ventral ones. Similar structures (one, two and sometimes three) can be found occasionally in the lungs of *B. brevicaudata, B. nchisiensis, B. perarmata, B. s. spectrum, B. s. boulengeri, B. supercilliaris* and *B. therezieni.* In the remaining species no trace of these enlarged alveolar walls is found. As to the gular pouch, this structure is absent in all species studied.



Figs. 1-6

Habitus of the lung.

Fig. 1, *B. brachyura;* fig. 2, *B. brevicaudata;*

fig. 3, *B. kerstenii;* fig. 4, *B. nchisiensis;*

fig. 5, *B. stumpffi;* fig. 6, *B. ebenaui.*

Miscellaneous anatomical observations

Some other anatomical peculiarities worth mentioning are the pigmentation of peritoneum, mesenteries and various internal organs. In 1977 I already mentioned the peritoneum and mesenteries of *B. marshalli* to be pigmented. In the other

Brookesia species examined this pigmentation is absent. A black pigmented gut is found in *B. betschi, B. brachyura, B. brevicaudata, B. griveaudi, B. kerstenii, B. nchisiensis, B. platyceps* and *B. spectrum boulengeri* (2 x). In the third specimen of this last species (MRAC 26653) and the remaining species the gut is unpigmented. Werner (1911 a) too found the gut of *B. s. spectrum* and *B. stumpfii* unpigmented. The oesophagus of all species examined is unpigmented. In contrast Werner (op. cit.) found the oesophagus of *B. s. spectrum* to be pigmented. Finally the testes are black pigmented in four African species (see above).

Discussion

The first thing to notice is the homogeneity in lungstructure within the genus *Brookesia*. Apart from the diverticula found in some African species, the lungs of all species studied are essentially the same, i.e. simple air sacs completely set with alveoles. Unfortunately well developed septa, as regularly found in *Chamaeleo*-lungs and representing very usefull taxonomic characters, are completely absent in *Brookesia*-lungs. Consequently it is not possible to delimit any groups within the present genus *Brookesia* with the help of lung-morphology. The same reasoning applies to such characters as the gular pouch and the pigmentation of peritoneum and mesenteries. Both characters are absent in all species studied with the only exception of *B. marshalli*, in which the last-named structures are pigmented. On the other hand the pigmentation of the gut and the testes and of presence of enlarged alveolar walls permit some grouping of the species. The (co-) occurrence of these characters (possibly in combination with the presence of diverticula) especially in East African species, e.g. *B. brachyura* and *B. nchisiensis*, is remarkable. When all species and their mutual relationship are considered, however, the grouping appears to be arbitrary and not resulting in natural groups.

The enlarged alveolar walls found in the lungs of various *Brookesia* species remind us of the small septa found in the lungs of some ordinary chameleons. In *C. fallax* Mocquard, 1900 and *C. guibei* Hillenius, 1959, for instance, the number as well as the size of the septa are rather small (see Klaver, 1977 text, the figures are erroneous as far as the septa are concerned). Moreover, the lungs of these species have some characters in common with those of *Brookesia*, viz. the shape of the lungs and the absence of diverticula. Werner (1911 a) already emphasized this resemblance in lung-structure between *C. fallax* and the two *Brookesia* species he studied, although he was mistaken about the subdivision of the lung-cavity in this and some other *Chamaeleo* species. He also noted, as had Beddard (1907) before him, that the simplicity in lung-structure correlates with the small size of the animals. The results of my studies on chameleon-lungs more or less support this view, as few or no diverticula and few or no septa are found in small to intermediate-sized species. Theoretically this might have been expected, as small-sized animals have a relatively large lung-surface area and probably can do without surface increasing structures such as septa. Therefore it is dubious to assume, as Werner (1911 a) does, that a simple lungstructure represents a primitive condition. Moreover, the rather simple lung-structure found in various distantly related *Chamaeleo* species, that cannot be considered primitive species, demonstrates that the lack of conspicuous lung-characters may be secondary (cf. Klaver, 1977). Finally the fact that chameleons of a more than average size, e.g. *C. jacksonii* Boulenger, 1896, have rather simple lungs (only one diverticulum and one large septum per lung), indicates that the surface/volume relation probably is but one of many factors determining the lung-structure. Other important factors may be, for example, respiratory efficiency, mechanical properties of tissues and ecological and behavioral requirements. It should be noted, incidentally, that the discussed simplicity in lung-structure may be apparent. Relying solely on lungs of presserved museum material, only rather straightforward macroscopic lung-characters could be studied and even these may be affected by poor preservation (cf. Klaver, 1977). Consequently very little can be said about how the lungs function. With the help of fresh material and microscopical and physiological techniques the simple lungs might prove themselves far more sophisticated structures than the ones with diverticula, etc.

Leaving the matter of primitiveness aside for the moment, we still have to decide whether the similarity in lung-structure between the Malagasy *C. fallax* c. s. and *Brookesia* species represents true relationship or is the result of parallelism. In favor of the first possibility are the following facts: First of all the chameleons concerned are distinguished by their small size. Next to that the *Chamaeleo* species are characterized by a flexible rostral protuberance. This character is also found in a number of African *Brookesia,* although the shape is somewhat different. Several African *Brookesia* species possess axillary pits, a character only found in Malagasy *Chamaeleo* species (but not all), including *C. fallax* c. s. Finally various characteristics of the East African *C. spinosus* Matschie, 1892, supposed to be the closest relative of *C. fallax* c. s., fit neatly in this argument. Next to its small size, flexible rostral protuberance and a tail shorter than head and body, the lungs of this species are truely *Brookesia*-like, i. e. no diverticula, no septa and only a few enlarged alveolar walls are present (Klaver, unpubl.).

Against affinity and thus in favor of parallelism is (next to the considerations concerning the various factors influencing the lung-structure already sketched above) the fact that the lungs of the closest Malagasy relative of *C. fallax,* viz. *C. nasutus* Duméril & Bibron, 1836, possess well developed septa. The same applies to the lungs of the supposedly closest continental relative of *C. spinosus,* viz. *C. tenuis* Matschie, 1892 (Klaver, unpubl.). The lungs, especially the septa, of this last species rather resemble those of *C. mlanjensis* Broadley, 1965 (cf. Klaver, 1977). The lungs of both *C. nasutus* and *C. tenuis* possess diverticula, but this trait is found in some East African *Brookesia* as well. From the above it appears to be hard to come to a decision as to relationship or parallelism. However, the discussion below will demonstrate, next to other things, that similarity due to parallelism is the more acceptable proposition.

It is likely that the pygmy chameleons evolved from a fully arboreal *Chamaeleo*-like ancestor. They still possess specialized adaptations to arboreal life, e. g. grasping feet, fused eyelids etc. (cf. the unrelated arboreal iguanid *Polychrus* species from South America). However, the prehensibility of the tail has been lost, probably because pygmy chameleons or their ancestors moved into a less extremely arboreal habitat (shrubs and undergrowth) or even reverted to the ground secondarily. This hypothesis of descent (!) is supported by the numerous characters various East African *Brookesia* species have in common with *Chamaeleo* species. Werner (1902 a and b) emphasized the osteological similarities, e. g. the sacral vertebrae are not fused to form a synsacrum in representatives of the two groups mentioned, whereas they are in the Malagasy *Brookesia*. The anatomical data presented in the present paper are in accordance with these observations: the presence of *Chamaeleo*-like diverticula, testes-, peritoneum- and mesenteries-pigmentation and hemipenes ornamentation in East African *Brookesia* is as remarkable as is the absence of these characters in Malagasy *Brookesia*. Of course it is self-evident that *Brookesia* of East Africa have more characters in common with their congeners of Madagascar, but their intermediate position as Werner (1902 a) called it is quite obvious.

The fact that especially East African *Brookesia* species occupy this intermediate position and that they seem to be more closely related to *Chamaeleo* than the *Brookesia* of Madagascar is not hard to explain considering the present theory concerning the origin and dispersal of chameleons (cf. Hillenius, 1959; Blanc, 1972 and Klaver, 1977 a.o.). According to this theory chameleons originated in East Africa and dispersed from here to the rest of the continent and by means of rafting to Madagascar. Only recently the plausibility of this theory was emphasized by the discription of a fossil chameleon from East Africa by Hillenius (1978). The *Brookesia* species evolved and dispersed on the African continent retained many ancestral characters, some species more than others. In contrast the Malagasy forms were subject to various important influences that made them loose their ancestral characters rapidly and develop their peculiar characteristics. Although descendants of the same East African stock, the Malagasy species originate from a small number of immigrants with a impoverished genetic makeup (founder principle). A parthenogenetic origin might even be possible (cf. Hall, 1970). Incidentally I expect it to be obvious from the content of the present paper, that separate origins of the African and Malagasy *Brookesia* as assumed by Hall must be rejected (see also Hillenius, 1963 and Bourgat, 1973). The absence of closely related species in East Africa and the many endemic species of Madagascar are indications that the number of immigrants was very limited indeed and that the majority of species are the result of autochthonous speciation. Moreover, both the original immigrants and their subsequent descendants had to adapt to and evolve under the quite different Malagasy conditions. Taken together these factors caused the Malagasy *Brookesia* to diverge radically from their continental relatives.

Owing to our almost complete knowledge of lung-morphology in *Chamaeleo*, we are able to infer that lungs with diverticula are to be considered primitive, whereas more simple lungs are secondary. The validity of this assertion results from the frequent occurrence of this character throughout this group and, moreover, from the positive correlation of this character with morphological characters, whose primitiveness already has been established (cf. Hillenius, 1959 and

Klaver, 1977). Therefore it is no surprise to find this primitive character only in the lungs of some East African *Brookesia* species. Lungs without diverticula are found in Malagasy as well as African species. It seems plausible that Malagasy *Brookesia* originate from the African forms that already lost their diverticula, as they have more characters in common, e. g. absence of testes pigmentation. Moreover, *B. nasus* is the only Malagasy species that next to these anatomical similarities, bears some resemblance with an African species, viz. *B. spectrum*. Both species possess, for example, some sort of flexible rostral protuberance and their frame is quite similar, "continental" so to speak (see also Brygoo et al., 1972). *B. spectrum* has the most extensive geographical distribution of all *Brookesia*, ranging from East to West Africa, and is not an unlikely candidate for migration to Madagascar. On the other hand the gross morphology of *B. nasus* and especially *B. nasus pauliani* Brygoo, Blanc & Domergue, 1972, point to affinity with the remaining *Brookesia* of Madagascar, in which the various characters are, however, often much more developed and modified (cf. Brygoo et al., 1972). Therefore I regard *B. nasus* a truely intermediate form between the remaining Malagasy and African species and a direct descendant of the original immigrants.

Finally I may add a few further remarks on lung-morphology. As to the septa it is immpossible to infer whether they were present in *Brookesia* lungs and were lost or they were absent from the very start. The fact that none of the species examined possess septa may be an indication in favor of the last possibility. However, the enlarged alveolar walls almost exclusive to and developed best in African forms, could be remnants of septa. Apparently there is no simple funtional interdependence between septa and diverticula as assumed by me in 1973. Lungs with septa may have or lack diverticula, whereas the same applies to lungs without septa. Diverticula could be linked in some way to arboreal life as other unrelated arboreal lizards, e. g. *Polychrus* and *Uroplatus*, have diverticula as well, but then still other arboreal lizards, including various *Chamaeleo* species lack them. Nevertheless the idea is worth considering, especially in view of our ignorance of lung-morphology in other groups.

Conclusion

In the present paper it is argued that our knowledge of the variation of taxonomic characters is too fragmentary to permit any conclusions as to the diagnostic value of these characters and, consequently, this renders systematic alterations at the genus level premature. If the necessary investigations to these characters are carried through, either even more striking differences will be discovered or other intermediate types will be found, thus bridging the gap between the more extreme forms. From the study of the lungs, the only anatomical structure studied comprehensively so far, it appears that the existing differences are gradual. Therefore I think the latter of the above possibilities the most credible at the moment and thus maintain the present classification of all pygmy chameleons in one genus, viz. *Brookesia*.

Acknowledgements

I thank the following colleagues for assistance with material on loan: Dr. D. Broadley (Umtali Museum), Dr. G. A. Ramanantsoa (University of Madagascar) and Dr. D. Thijs van den Audenaerde (Musée Royal de l'Afrique Centrale). I am also most grateful to Prof. Dr. J. Guibé for fascilities granted while working at his institution (Muséum National d'Histoire Naturelle). I am especially indebted to Dr. Ramanantsoa, who generously provided me with valuable information in advance of the proper publication and to Dr. W. Böhme (Zoologisches Forschungsinstitut and Museum Alexander Koenig, Bonn, Germany) for the opportunity he gave me to verify some anatomical facts and offering valuable suggestions.

Summary

In order to evaluate the systematic status of the genus *Brookesia* Gray, 1864 the systematic alterations (often without argumentation) by previous authors and the diagnostic value of the various taxonomic characters used are discussed. Some personal observations on these characters are included in this discussion. It appears that the status of the genus *Brookesia* as well as its relation to the second genus within the family Chamaeleonidae that is currently distinguished, viz. *Chamaeleo* Laurenti, 1768, is still uncertain.

As previous studies on chameleon-lungs demonstrated lung-characters to be very useful to the taxonomy, a comprehensive study of *Brookesia* lungs was made in order to provide new arguments for the systematic discussion of this group.

Zusammenfassung

Um den systematischen Status der Gattung *Brookesia* Gray, 1864 aufzuhellen, werden die bisherigen (oft ohne Argumente erfolgten) Klassfikationsvorschläge früherer Autoren sowie der diagnostische Wert der bislang benutzten taxonomischen Merkmale diskutiert. Eigene Beobachtungen zu diesen Merkmalen werden in die Diskussion einbezogen. Dabei zeigt sich, daß der Status der Gattung *Brookesia* und deren Beziehungen zu *Chamaeleo* Laurenti, 1768, der zweiten heute allgemein unterschiedenen Gattung innerhalb der Chamaeleonidae, noch unsicher ist.

Da frühere eigene Studien an Chamäleon-Lungen die Nützlichkeit lungenmorphologischer Merkmale für taxonomische Ziele demonstrierten, wurde eine umfassende Untersuchung von *Brookesia*-Lungen durchgeführt, um der systematischen Diskussion um diese Gruppe neue Argumente zu liefern.

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